

First known axis vertebra of a madtsoiid snake (*Yurlunggur camfieldensis*) and remarks on the neck of snakes

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ABSTRACT

The cervical vertebrae of basal fossil snakes are important objects of study for clarifying the pattern and process of the evolutionary transition from tetrapodal (lizard) ancestors. This transition has recently been addressed in studies of developmental genetics as well as phylogeny-based comparative analyses of limb-reduced lizards, without apparent resolution. An axis (second cervical) vertebra of a large snake from the Camfield Beds, Northern Territory (Bullock Creek Local Fauna, Middle Miocene) is attributed to the holotype skeleton of *Yurlunggur camfieldensis* Scanlon, 1992 (Madtsoiidae). It is the first axis known from this extinct family, but is likely to provide useful taxonomic data when those of other species are identified. As well as similarities to primitive extant snakes of several families, some features resemble those of certain varanoid lizards.

KEYWORDS: snake, Madtsoiidae, *Yurlunggur*, cervical vertebrae, Miocene, Northern Territory.

INTRODUCTION

Yurlunggur camfieldensis Scanlon, 1992 is a large, extinct snake known only from the Blast Site locality, Camfield Beds, Northern Territory (Bullock Creek Local Fauna, Middle Miocene; Woodburne *et al.* 1985; Murray and Megirian 1992). All of the madtsoiid remains so far known from the site (vertebrae and ribs) are consistent with a single skeleton, and collectively identified as the holotype of this taxon (Scanlon 1992). Many other specimens referred to *Yurlunggur* are known from various deposits at Riversleigh, north-western Queensland, and single or few vertebrae from other localities in northern South Australia, eastern Queensland, and western New South Wales (Table 1). All of this material is either indeterminate as to species, or regarded as belonging to species distinct from *Y. camfieldensis*, but as yet undescribed (Scanlon 1996, 2003; and unpublished).

Other snake remains from the Bullock Creek LF (several localities) represent multiple individuals of a somewhat smaller pythonine boid originally described as *Morelia antiquus* Smith and Plane, 1985, but now referred to *Morelia riversleighensis* (Smith and Plane, 1985) (Scanlon 2001). A single incomplete vertebra of an indeterminate elapid snake has also been reported (Scanlon 1992; Scanlon *et al.* 2003).

Among elements of the *Y. camfieldensis* skeleton mentioned previously, but not fully described, is the axis vertebra (Scanlon 1992: 58). This is the first axis known from any member of the Madtsoiidae, and thus allows the

first comparison of a number of characters between this family and other squamates.

Additional characters for madtsoiid snakes are of interest because there is evidence that this Gondwanan group, with a fossil record beginning in the early Upper Cretaceous (Rage and Werner 1999), represents an archaic lineage phylogenetically close to the origin of the two major extant groups (Scolecoophidia and Alethinophidia; Scanlon 1993b; Rage 1998), and probably lying outside this dichotomy. This phylogenetic position was implied by Hoffstetter (1961), asserted by McDowell (1987), and inferred by parsimony analysis in Scanlon and Lee (2000) and Lee and Scanlon (2002a). After extinctions in the other Gondwanan continents during the Eocene, madtsoiids had a relictual distribution in Australia where a number of genera are known in the Miocene, of which two (*Wonambi* and *Yurlunggur*) persisted to the Pleistocene (Scanlon 1993a, 1995, 1997; Rage 1998; Mackness and Scanlon 1999; Scanlon and Lee 2000).

MATERIALS AND METHODS

Snake remains reported previously from Bullock Creek (Scanlon 1992, 1996) were studied on loan at the Vertebrate Palaeontology Laboratory, School of Biological Sciences, University of New South Wales. Several additional vertebrae of *Y. camfieldensis* have been identified subsequently (examined briefly in Darwin in 2003), and more pieces of the holotype skeleton may remain unidentified in concentrate that is not yet thoroughly sorted (D. Megirian pers. comm.).

The most anterior vertebra in squamates, the atlas, consists of a ring formed by the paired (or sometimes fused) tecta of the neural arch, and the first pro centrum (Romer 1956; Hoffstetter and Gasc 1969). The body of the second vertebra, the axis, is formed by three fused elements belonging to the first and second cervical segments: first centrum (odontoid process), second centrum (axial centrum proper), and second intervertebral ring (condyle, articulating with the cotyle or glenoid cavity of the third vertebra). The axis bears two hypapophyses, which originate as hypocentra of the first and second vertebrae; the second fuses to the axial centrum, while the first usually has only a sutural attachment but is sometimes fused, e.g., in most Uropeltinae (Williams 1959). Varying positions have been taken on whether any vertebrae posterior to the axis can be included in the 'cervical' region, and this question is discussed below ('Remarks on the neck in snakes').

Comparisons are based on figures and descriptions in the literature, skeletal material of recent squamates (listed below), and fossils of other Australian madtsoiids. Institutional abbreviations used: AMNH = American Museum of Natural History; AM R = Australian Museum herpetology; AR = Archer reference collection, University of New South Wales; MM R = Macleay Museum, University of Sydney; NMV P = Museum of Victoria palaeontology; NTM P = Museums and Art Galleries of the Northern Territory palaeontology; QM F = Queensland Museum palaeontology; QM J = Queensland Museum herpetology; SAM P = South Australian Museum palaeontology.

Comparative material

- Aspidites melanocephalus* – QM J30786.
A. stimsoni – uncatalogued (Alice Springs, NT).
Liasis mackloti – uncatalogued (Fogg Dam, NT; coll. R. Shine *et al.*).
Python molurus – AMR 366.
Varanus varius – AR 5378.
Heloderma suspectum – AMNH Field Series 109521.
Anguis fragilis – UNSW Bioscience teaching collection (tag IV 6.4.4101).
Austrelaps ramsayi – uncatalogued (Bowral, NSW).

DESCRIPTION AND COMPARISON

The axis (NTM P908-4, Fig. 1) is incomplete but well-preserved, without distortion or surface wear; almost all structures are preserved intact on one side or the other. There is a close fit between the condyle of the axis and the cotyle of the most anterior known trunk vertebra (NTM P895-5, Fig. 1; also illustrated with other trunk vertebrae in Scanlon (1992: fig. 1A)); because dimensions of the condyle and cotyle generally increase steeply with sequential position in this region of the other snake skeletons examined, the fit with the axis implies that P895-5 is the third cervical (or first 'trunk') vertebra. The main areas of damage on both bones (left side of the axis neural arch, and right prezygapophysis and zygosphenes of the other vertebra) are consistent with results of a single torsional force imposed during disarticulation of adjacent elements.

Table 1. Occurrence of *Yurlunggur* (Madtsoiidae) in Australian fossil assemblages. Abbreviations: Fm, Formation; LF, Local Fauna.

Locality	Formation / Local Fauna	Nominal age	Date reference	Species	Record reference
Tom O's Quarry, Lake Tarkarooloo, SA	upper Namba Fm / Tarkarooloo LF	Late Oligocene	Rich <i>et al.</i> 1991 Woodburne <i>et al.</i> 1993	<i>Y. sp. indet.</i>	Scanlon unpubl.
Riversleigh World Heritage Area, NW Qld (multiple sites)	'Carl Creek Limestone', Systems A, B, C / multiple LFs	Late Oligocene – Middle Miocene	Archer <i>et al.</i> 1989, 1997	<i>Y. spp.</i> (2 or more unnamed)	Scanlon 1992, 1996, 2003
Leaf Locality, Lake Ngapakaldi, SA	Wipajiri Fm / Kutjumarpu LF	Early or Middle Miocene	Rich <i>et al.</i> 1991	<i>Y. sp. indet.</i>	Scanlon 1996
Blast Site, Bullock Creek Stn, NT	Camfield Beds / Bullock Creek LF	Middle Miocene	Woodburne <i>et al.</i> 1985; Murray and Mcgiran 1992	<i>Y. camfieldensis</i>	Scanlon 1992
Stirton Quarry, Lake Kanunka, SA	lower Tirari Fm / Kanunka LF	Pliocene	Tedford <i>et al.</i> 1992	<i>Y. sp. indet.</i>	Pledge 1992; Scanlon unpubl.
Chinchilla Rifle Range, Condamine River, western Darling Downs, S Qld	Chinchilla Sands / Chinchilla LF	Early or 'Middle' Pliocene	Rich <i>et al.</i> 1991, Mackness 1995	<i>Y. sp. indet.</i>	Mackness and Scanlon 1999
Wyandotte Creek, NE Qld	Wyandotte FM / Wyandotte LF	Late Pleistocene	McNamara 1990	<i>Y. sp. indet.</i>	McNamara 1990; Scanlon 1995
Gogolo-Garpung lunette, Willandra Lakes, W NSW		Late Pleistocene	J. Hope pers. comm.	<i>Y. sp. indet.</i>	Scanlon unpubl.

The first axial hypapophysis is not preserved, having separated from the centrum at the suture; some fusion of the elements may have been present but it was evidently minor in extent. The attachment surface on the centrum is formed by horizontal and vertical portions, forming a right angle in lateral view (broadly obtuse or less angular in most squamates, but similar in mosasaurs; Russell 1967). The ventral-facing portion (probably formed entirely by the odontoid element) is a flattish area irregularly defined by the remains of the suture, forming a rough triangle notched anteriorly by an extension of the articular surface of the odontoid process, and truncated posteriorly by the vertical surface of contact with the second hypapophysis (thus, like a broad ∇). A recessed area in the ventral half of the vertical portion is an exposed sinus within the vertebra; part of the lower rim has been broken away, possibly during excavation or processing, as the broken surface is pinkish white rather than dark grey like the rest of the surface. The rest of this anterior face, and the adjoining ventral face, have a roughened and pitted surface.

The fusion of the odontoid process with the axial centrum posterior to it is not complete, as a transverse suture can be seen on the dorsal surface (just anterior to the subneural process, the bridge-like structure in the ventral midline of the neural canal). The line of fusion is defined laterally only by a groove or slight constriction, which meets the vertical suture with the missing hypocentrum.

The anterior articulating surface of the odontoid process forms a convex hexagon slightly wider than high in anterior view; the odontoid element itself extends for the full width, and the suture or line of fusion with the second centrum is not visible anteriorly. The articular surface is not distinctly subdivided, but an inflection of its curvature and slight transverse ridge suggest a boundary of central (anterodorsal) and peripheral (lateral and ventral) areas. The central area forms a partial ellipsoid, with a transverse curvature similar to the condyle of the same vertebra (compare in dorsal view, Fig. 1), but in lateral view shows an almost straight anteroventral edge. Dorsally, the process is concave, with an upturned rim, weak laterally but prominent and sharply defined anteriorly (differing from other snakes examined, where the rim is high laterally but notched anteriorly).

In many snakes (e.g., *Python molurus* of approximately equivalent size to *Y. camfieldensis*), the articular surface of the odontoid is triradiate in form, separated clearly by sutures into central, lateral and ventral areas (the ventral section belonging to the first hypapophysis and articulating with the first intercentrum, and lateral sections belonging to the main axial centrum and articulating with the neural arch). The condition in *Yurlunggur* differs from most lizards and snakes examined, but resembles that in *Heloderma*

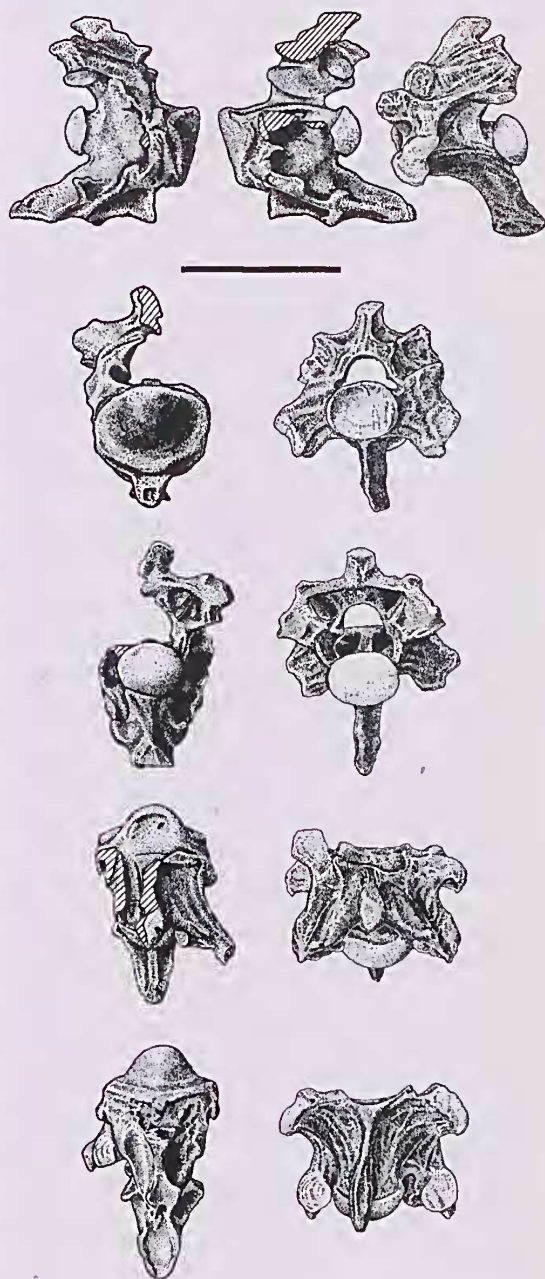


Fig. 1. Axis (NTM P908-4, left) and third cervical vertebra (P895-5, right) of holotype *Yurlunggur camfieldensis* Scanlon, 1992, from Blast Site, Camfield Beds, NT (Bullock Creek Local Fauna, Middle Miocene). From top to bottom: lateral (right and left sides of P908-4, left side of P895-5), anterior, posterior, dorsal, and ventral views. Diagonal lines indicate broken surfaces. Scale bar = 20 mm.

(pers. obs.) and Xenosauridae (*Shinisaurus* and *Xenosaurus*: Hecht and Costelli 1969). It is not certain whether the first hypapophysis bore an extension of the articulating surface, but as the lower edge of the preserved part of the facet is convex ventrally (as in *Heloderma*; not concave as in *Anguis*, *Varanus* or *Python*), there seems no reason to suppose that it did.

The atlas-axis joint of snakes allows for some twisting about the spinal axis, so that the prezygapophyses and zygosphene (which strictly limit twisting in most of the column) do not have the same form or function as in trunk vertebrae. In *Varanus* and xenosaurids, acute triangular processes project anteriorly on either side of the neural canal (apparently in serial homology with the prezygapophyses), and pass medial to the aliform processes to engage separate ventral recesses in the atlantal arches, in the manner of a zygosphene-zygantrum joint. The processes of the axis have dorsolateral facets, but there are no distinct opposing facets in the 'zygantra' (at least in *Varanus*). In most snakes, the anterior edge of the neural arch forms a broader and less prominent shelf (more like a zygosphene) which fits under the posterior edge of the atlantal arches, the contact defining an arc centred within, or even below, the odontoid process. In *Python*, this area of contact extends across the midline of the axis, and is only weakly defined posteriorly; but in *Yurlunggur*, like many other snakes, the shelf is interrupted on the midline, while the contact with the atlas is strongly limited by an overhanging median projection of the axial neural arch. Such an overhang (by the anteriorly prolonged neural spine) is present in *Anguis*, xenosaurids, varanoids, and some colubroids, but not in scolecophidians (Evans 1955), aniiloids (Williams 1959; Rieppel 1979) or pythonines. An unusual feature in *Yurlunggur* is that the anterolateral shelf is not simply notched medially, but continues internally as a longitudinal crest defining a distinct mid-dorsal lobe of the neural canal. A similar internal dorsal groove is moderately distinct in the axis of *Heloderma suspectum* and weakly defined in an elapid, *Austrelaps rousayi*, but absent in all the other squamate species compared.

Apart from the absence of parazygantral foramina, the zygantrum and postzygapophysis present no qualitative differences from those of the immediately following vertebra (NTM P895-5), but the neural spine and dorsolateral processes differ in proportions. The neural spine is about as high as that of the third vertebra (i.e., very low compared to *Python*, but comparable to members of most other snake lineages), but its upper part is considerably more expanded both laterally and posteriorly. Above the postzygapophysis are two processes for muscle or tendon attachment. The more dorsal of these is somewhat smaller, while the more lateral is much more prominent posteriorly, than the

corresponding structures on the next vertebra. The aliform processes are only weakly differentiated into inner and outer members in *Python*, and not at all in *Austrelaps* or *Acanthophis*.

In place of the laterally prominent cylindrical transverse processes borne by the axis of *Python*, the axial 'ribs' of *Yurlunggur* are short spines directed posteriorly (preserved on the left side only). However, these spines are mounted on buttresses which extend ventrally from the sides of the neural arch (where they are continuous with the interzygapophyseal ridge and hence postzygapophyses), then posteriorly along the sides of the hypapophysis. The vertical posterior face of the buttress has two pits on each side, containing foramina. There are two processes projecting dorsally from the longitudinal part of the buttress on each side, the more anterior also flanking deep (dorsoposterior-facing) pits and foramina, while the more posterior (below the condyle) are simpler in shape, like dorsally concave hooks. These and the other paired lateral processes of the hypapophysis differ in details of shape between the sides, but not so much as to indicate gross abnormality of the vertebra. The hypapophysis then continues posteriorly as a narrow keel with a slightly thickened ventral edge, before bifurcating to form ventrolateral prominences defining concave lateral and ventral surfaces beside and between the ridges. This pair of processes is just below the second pair on the lateral buttresses, level with the condyle. Behind them, the ridges reapproach to border a large posteroventrally directed median subcentral foramen, then again diverge, fuse with the lateral buttresses, and enclose a concave elliptical surface, extending to the posterior end of the hypapophysis.

The dorsal and lateral faces of the hypapophysis are simple and smooth in structure, the dorsal edge being similar in lateral profile to that of the third vertebra, only more oblique; it is not sharp, but expanded below the condyle to merge with the centrum, and posteriorly to form a ploughshare-like shape where it merges with the ventrolateral ridges.

Between the two processes on each side are another pit and foramen, facing anterolaterally. Thus, *Yurlunggur* has two pairs of pits on the lateral surface of the axis, whereas only one pair of pits (for muscle insertion) is present in *Python*. More typical lateral foramina are also present, level with the lower edge of the condyle. A pair of foramina occurs in the hollows posterolateral to the transverse expansion of the hypapophysis.

In general, though not in all details, this complex hypapophysis can be compared with that of *Shinisaurus* (Hecht and Costelli 1969). The morphology of the axial hypapophysis of *Python* (like most other squamates) is much simpler: there is a simple ventral keel without bifurcation or foramina; weak lateral ridges are present, defining upper and lower lateral faces of the

hypapophysis, but they can not be considered continuous even as far as the muscle insertion pit, and do not approach the 'rib' which is thus a free process and not part of a 'buttrass'.

Comparisons among extant squamates show that the axis varies considerably in proportions, and shape and extent of processes and articulating surfaces, at a low taxonomic level, for example within Xenosauridae (Hecht and Costelli 1969), within Uropeltidae (Williams 1959, Rieppel 1979) and within Pythoninae and Elapidae (pers. obs.). Therefore no detailed character analysis has been attempted in comparing the axis of *Yurlunggur* with examples in other families; nevertheless, there is a strong general resemblance to those of *Cylindrophis* and *Anilius* (Williams 1959: fig. 4; Rieppel 1979: fig. 9). Differences from these genera and all others examined are the strong lateral and ventrolateral crests of the hypapophysis, and the distinct median dorsal channel in the neural canal, interrupting the anterodorsal articulating surface.

In addition to the 29 vertebrae and various rib fragments described or mentioned previously (Scanlon 1992, including 'Note added in proof'), three nearly complete trunk vertebrae and one more fragmentary specimen from Blast Site are attributed to the holotype of *Y. camfieldensis*. NTM P904-4 is a part of the neural arch consistent with an anterior trunk vertebra; P999-1 is a mid-trunk vertebra approximately equal in size and regional features to the largest element identified previously (P908-1; Scanlon 1992: 58); and P895-131 and P991-26 are posterior trunk vertebrae intermediate in size and regional features between P8692-28 (No. 17) and P8695-247 (No. 18). A posterior trunk vertebra previously listed with the 'block' registration P895-245 is now individually registered as P895-26.

REMARKS ON THE NECK IN SNAKES

In snakes, the term 'cervical' is often restricted to the atlas and axis (de Rochebrune 1881; Hoffstetter and Gasc 1969), because the complete loss of the shoulder girdle and sternum precludes applying the traditional definition for the cervical-thoracic boundary. Thus, it has often been considered that "we have no knowledge of how long the neck is in snakes, in the absence of any differentiation between cervical and thoracic column" (McDowell and Bogert 1954: 61; similar views are expressed by Nopesa 1908 [but not Nopcsa 1923, 1925], Camp 1923; Bellairs and Underwood 1951), but this proposition is questionable (see also Caldwell 2003).

In the snake embryo, only the atlas is distinctive in gross morphology, while the axis closely resembles the succeeding anterior trunk vertebrae (Cohn and Tickle 1999: fig. 1) except in rib length, which increases posteriorly through this region as it does in adults.

According to Cohn and Tickle (1999):

The anterior vertebrae have both ribs (a thoracic feature) and ventral hypopophyses (generally a cervical feature)...., suggesting that information encoding thoracic identity may have extended into the cervical region and partially transformed these segments. Thus, the entire trunk resembles an elongated thorax.

However, cervical ribs are plesiomorphic and widespread in amniotes, including lizards (Romer 1956; Hoffstetter and Gasc 1969; Gaffney 1985), so their presence in snakes actually implies no such transformation. Most lizards have free (articulated) ribs beginning at the third or fourth cervical vertebra, though some have them present even on the axis; snakes show exactly the same range of variation (Hoffstetter and Gasc 1968, 1969; Scanlon 1996).

There is unquestionably a *relative* lack of distinction between neck and thorax in snakes, and this represents one of the main features of their evolutionary transformation from tetrapodal lizard ancestors. Rather than an extension of 'thoracic identity' into the cervical region (as proposed by Cohn and Tickle 1999), it may be better described as an extension of 'cervical identity' into the thorax. Nopesa (1925) suggested that the latter was important in the origin of snakes and (in line with his neo-Lamarekist view of evolutionary process) occurred not suddenly but gradually over a long period:

If one proceeds from the assumption, supported by the chronological succession, that the similarity of the presacral vertebrae of the specialised chelonians and the alethinophidians is not simply a convergence phenomenon, but rather is genetically conditioned, then one sees positively how the origin of snakes proceeds, *though not on land, rather in a shallow near-coastal sea*, from Neocomian to Eocene gradually [and] cranio-caudally, and is only half-attained in the Cenomanian (emphasis in original German; trans. Scanlon 2000).

'Cervicalization' of the trunk is also obvious from the presence of hypapophyses not only on the 40–70 anterior vertebrae in most snakes (Caldwell 2000), but throughout almost the whole trunk in various modern lineages – at least this is obvious once we have shaken off (as, eventually, did Hoffstetter (1968)) the idea that hypapophyses on trunk vertebrae are somehow retained from amphibian-grade ancestors despite their absence in nearly all amniotes. Neither of these 'diffusion' processes implies that the cervical region no longer exists (*contra* the interpretation of Cohn and Tickle's work by Rieppel *et al.* (2003)), only that the cervical-thoracic boundary has become relatively subtle in extant snakes.

There is a real question of homology here as well as a difficulty of definition, as many other limb-reduced reptile lineages have distinct but short cervical regions (with shoulder vestiges and thoracic organs close

behind the head), and some authors have considered snakes to be closely related to one of the lineages of short-necked burrowing lizards (e.g., Rage 1982 [but not Rage 1997]; Senn and Northcutt 1973; Greer 1985 [but not Greer 1989]; Cundall *et al.* 1993). Greer (1989) drew attention to the sharp discontinuity in morphology between the elongate and nearly limbless pygopodid lizards and their nearest living relatives, the geckoes, which show no trend to elongation or limb reduction; he suggested that a rapid transition in body form may have occurred, and that snakes may have been derived from terrestrial varanoids by an analogous (but unknown) mechanism:

In structure, but not habits, snakes would represent the stretched version of varanoids just as pygopodids are the stretched version of geckos (Greer 1989: 219).

Cohn and Tickle (1999) proposed that a change in expression of *Hox* genes (which they demonstrated in comparison of snake and chick embryos) provided a common evolutionary mechanism for loss of the forelimbs and elongation of the trunk in ancestral snakes. This has been investigated by study of various lizard groups which have independently evolved a snake-like body form (pygopodids, anguids, amphisbaenians, and many others). Apart from snakes, all such groups with reduced limbs and greatly increased numbers of vertebrae retain at least traces of the shoulder girdle (and normal-length or short necks), and this has been considered to refute the Cohn and Tickle model (Wiens and Slingluff 2001).

Whether or not there is a known signalling molecule that shows a clear demarcation of expression between the regions in early snake embryos (Cohn and Tickle (1999) found an absence of evidence, not *vice versa*), many snakes do have a more or less distinct transition in vertebral (and rib) proportions close to the position of the heart, so that the whole 'anterior trunk' or 'precardiac' region (Hoffstetter and Gasc 1969; Gasc 1974; LaDuke 1991), comprising 40–70 vertebrae with prominent hypapophyses in extant lineages, is sometimes referred to as 'cervical' (e.g., Ivanov 2002). Some aspects of regional differentiation may be largely epigenetic in certain taxa, resulting from chemical or mechanical interaction among parts during ontogeny rather than an initial 'blueprint', but that does not make them unreal.

One approach to locating (rather than denying or obfuscating) the cervical-thoracic boundary in snakes is to consider the position of the heart or lungs (e.g., Nopcsa 1923; Caldwell 2000), rather than any musculoskeletal vestige of the shoulder girdle (which has been sought in vain). It was recognised quite early that the 'neck' of quadrupeds could be defined in alternative ways based either on its functions or its anatomical relationships:

Another part present in these animals [oviparous quadrupeds] is a neck, this being the necessary consequence of their having a lung. For the windpipe by which the air is admitted to the lung is of some length. If, however, the definition of a neck be correct, which calls it the portion between the head and the shoulders, a serpent can scarcely be said with the same right as the rest of these animals to have a neck, but only to have something analogous to that part of the body. (Aristotle. *On the Parts of Animals*, Book IV Ch. 11, trans. Ogle 1941)

In this passage, Aristotle did not state that snakes have no neck, but made it clear that (even for him, the arch-dichotomist) this was a question of partly arbitrary definition rather than fact. Snakes have lungs (or at least one lung) and a windpipe (trachea), and the position of tracheal entry to the lung, had Aristotle dissected as many snakes as Wallach (1998), might have appealed to him as a reasonable alternative criterion for definition of the neck. Whatever single criterion may be selected or uncritically adopted from ancient authorities, in fact the terms 'neck' and 'cervical' are abstractions with numerous components when applied to limbed vertebrates, of which some certainly can be evaluated in snakes (Caldwell 2000). The study of snake vertebral columns, particularly those of potentially 'transitional' fossils, is essential for a full understanding of these questions.

The probable nearest living limbed relatives of snakes (varanid lizards) have quite long necks, with the cervical vertebrae usually increased in length as well as slightly elevated in number, but the heart is also in an unusually posterior position within the thorax (Bellairs and Underwood 1951) so that the heart's position may be a poor guide to 'true' neck length in snakes. Dolichosaurs (small, elongate, Cretaceous marine varanoids possibly forming the stem-group of snakes) had a further increased number of cervical vertebrae (Nopcsa 1908, 1923; Bellairs and Underwood 1951; Caldwell 2000; Lee and Caldwell 2000), and some Cretaceous fossil snakes have been interpreted as having a more distinct neck than modern forms (Nopcsa 1923; Lee and Caldwell 1998; Lee *et al.* 1999), but this needs to be tested by more detailed and quantitative comparisons. A view that snakes have short necks is apparently correlated with support for the 'small fossorial' model of snake origins, whereas long necks make sense in terms of varanoid relationships and possible aquatic ancestry (Nopcsa 1923, 1925; Scanlon *et al.* 1999; Caldwell 2000; Lee and Scanlon 2002b).

DISCUSSION

While *Yurlungur* became extinct only in the Quaternary (Table 1), Madtsoiidae is one of the oldest snake lineages known (Rage and Werner 1999) and in some respects, among the most primitive (McDowell 1987; Scanlon 1996; Scanlon and Lee 2000; Lee and Scanlon 2002a; Scanlon 2003).

Comparisons with primitive extant snakes and other early fossils are needed to determine to what extent the specimen described here represents the ancestral morphology of the snake axis, and how far it is independently specialised. The axis of *Yurlunggur* resembles those of *Anilius scytale*, *Cylindroplis ruffus* and *C. maculatus* to about the same extent that these anilioid species resemble each other, so that it can be considered to represent approximately the same 'grade' of primitive snakes, but more detailed comparisons are not presently justified in view of the divergent specialisations of anilioids in this element (see above). The axis of the Late Cretaceous aquatic snake *Pachyrhachis* has been partially described (Lee and Caldwell 1998) and it seems to be similar to *Yurlunggur* in possessing a relatively short centrum, low, posteriorly directed neural spine, and massive, posteriorly directed hypapophysis. This element is unknown in *Pachyophis* (Lee *et al.* 1999), and although preserved in *Haasiophis* (Rieppel *et al.* 2003) and *Dinilysia* (Caldwell and Albino 2002), no morphological details are yet available.

In comparison with lizards, there are particular resemblances to *Heloderma* and to mosasaurs rather than to anguimorphans or varanoids in general. The anterior articulating surface of the centrum is convex and limited to the odontoid element, as in *Heloderma*, rather than distinctly triradiate and extending to the axial centrum proper as in the other lizards and snakes compared. The neural canal has a distinct internal dorsal groove, again the nearest approach being in *Heloderma*. The surface for attachment of the anterior hypapophysis forms a right angle in lateral view, as in some mosasaurs, but is broadly obtuse in other lizards and snakes.

This is the first axis reported for any member of Madtsoiidae, and without knowledge of this element in other madtsoiids or definite close outgroups, no particular phylogenetic or functional significance can yet be attributed to the features reported here. While it does not resemble those of either *Varanus* or lizards in general more than it does extant snakes, certain unusual features shared with mosasaurs and *Heloderma* may provide support for the hypothesis of varanoid-snake affinities. Given the extent of variation in this element among related species and genera of extant squamates, morphology of the axis is likely to contribute valuable diagnostic and phylogenetic information within Madtsoiidae when more examples become known.

The identification of additional trunk vertebrae from Blast Site subsequent to the initial description, but not from other exposures in the Camfield Beds, has been interpreted as statistical confirmation that all *Yurlunggur* remains from the deposit represented a single skeleton (Scanlon 1992: 59). This pattern has continued; although only a few additional vertebrae have been identified in the last decade, they remain consistent with one individual. Two of the newly identified vertebrae come from one of the significant 'gaps' in the column as

previously known (between Nos 17 and 18; Scanlon 1992: 59), raising hopes that parts of the skull and caudal region may remain to be identified among material from Blast Site.

The representation of well-preserved mid-trunk vertebrae allows a relatively precise (though not necessarily accurate) estimate of total length. Using the ratio of maximum vertebral width (across the prezygapophyses, 46.4 mm in P908-1; Scanlon 1992) to total length of the vertebral column adopted as a 'standard' (1:136.9 in a skeleton of the python *Aspidites melanocephalus*; Scanlon 1993a), and adding head length of approximately 150 mm (cf. *Wonambi naracoortensis*; Scanlon and Lee 2000), the total length of *Y. camfieldensis* in life can be estimated as 6.5 m. This would be larger than any authenticated extant snake in Australia (e.g., Greer 1997) or any *Yurlunggur* fossils from Riversleigh, but *Y. camfieldensis* was apparently exceeded in size by a Pleistocene species of *Yurlunggur* from north-east Queensland as well as the Pliocene python *Liasis dubudingala* (Scanlon 1996; Scanlon and Mackness 2002).

As discussed above, modification of the neck of snakes has long been considered an important aspect of their transformation from lizards, but no consensus has been reached as to the processes and stages involved. Apart from the type of *Y. camfieldensis*, multiple associated or partly articulated skeletons of madtsoiids are now known from Australia, including several partial skeletons of *Yurlunggur* spp. from Riversleigh (Scanlon 1996, unpublished data), and recently discovered articulated 'cervicals' of *Wonambi naracoortensis* (M. Hutchinson and E. Reed pers. comm.) as well as the disarticulated partial skeletons of this species previously reported (Barrie 1990). Further study of this material will provide detailed information on qualitative and quantitative variation in vertebral morphology along the column. The pattern of intracolumnar variation in the trunk of madtsoiids is likely to retain plesiomorphic features lost in all modern snakes, as has already been confirmed in the those of the skull and the caudal vertebrae (Scanlon and Lee 2000). Australian madtsoiids may be just the transitional fossils needed to unlock this important and controversial evolutionary question.

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